

PARASITISM OF SINGLE AND MULTIPLE EGG CLUSTERS OF
EUPHYDRYAS PHAETON (NYMPHALIDAE)

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Abstract.—The effect of egg numbers on parasitism of *Euphydryas phaeton* (Nymphalidae) was examined by comparing single and multiple egg clusters on leaves. Some 65 to 80% of the clusters lost eggs to parasitism and predation, with 5 to 9% of the eggs lost per cluster. For total clusters, single clusters and multiple clusters, the numbers of parasitized clusters were significantly different between years. It appeared that when the overall level of parasitism was greater one year, multiple clusters were attacked more frequently than single clusters. However, the number of egg clusters per leaf had no effect on the number of parasitized eggs per cluster. The sequence of egg clusters deposited on a leaf did not affect the level of parasitism and number of parasitized eggs per cluster. Thus, these egg clusters composed of several hundred eggs each lost only a small fraction of eggs to parasitoids and predators and did not appear to benefit from aggregation of egg clusters.

Introduction

The patterns of egg distribution by insects are varied; with some insects depositing eggs singly, others depositing many small clusters of eggs, and others laying a few large clusters. Eggs deposited in clusters may have higher survivorship than those laid singly (Stamp 1980a). Furthermore, parasitoids may differ in their efficiency at exploiting various sizes of egg clusters (Hokyo and Kiritani 1966). Egg parasitoids specializing on a host depositing eggs singly, attacked fewer eggs when those eggs were clustered, as a consequence of reduced encounters with total host eggs and limited mature eggs for oviposition (Hirose et al. 1976). In contrast, for parasitoids adapted to eggs occurring in clusters, large clusters were found more frequently and had higher parasitism than small clusters (Lyons 1962). This may be a consequence of the searching behavior of animals which concentrate their efforts in areas where they recently found prey (Laing 1937, Tinbergen et al. 1967, Royama 1970). Also, as immobile host patches, large clusters may be advantageous to parasitoids and predators as the overall distances between clusters increases (e.g. Janzen 1975). Thus, egg parasitoids searching for large egg clusters may deposit all or most of their eggs in one or a few places

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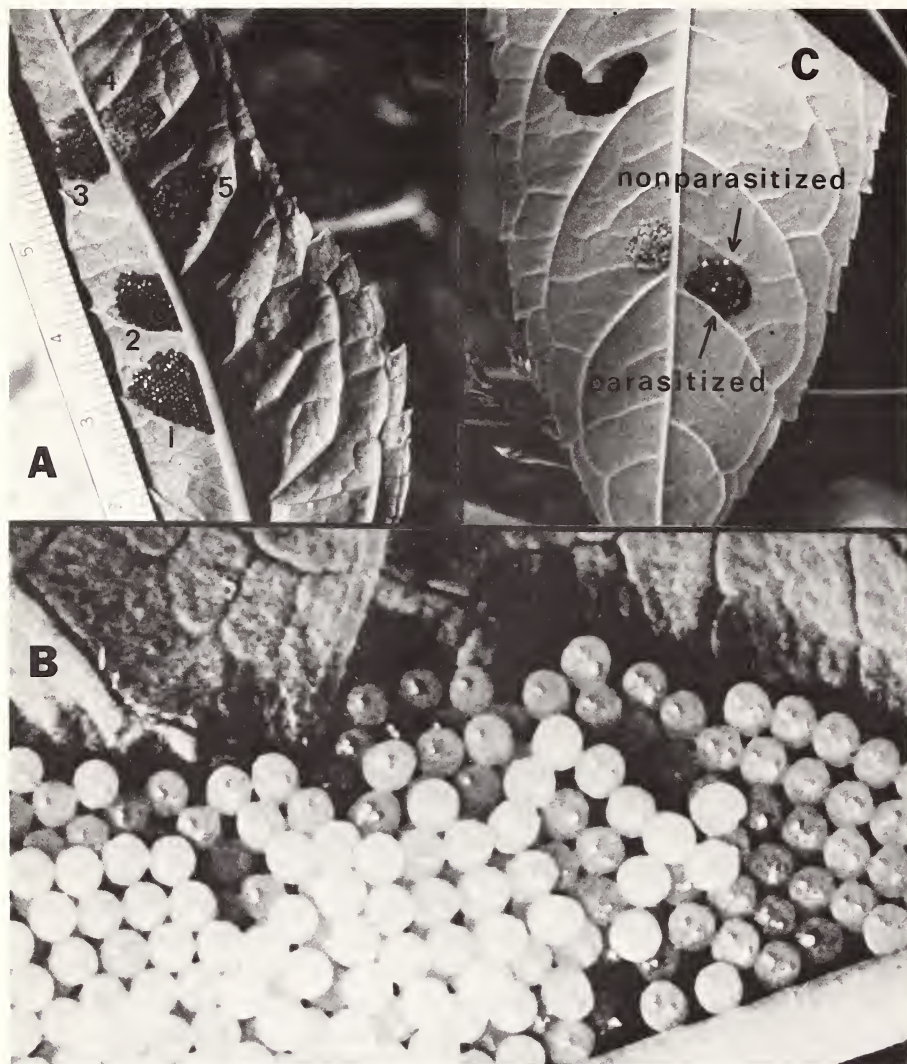


Fig. 1. Egg clusters of *E. phaeton*. A. Five clusters deposited on the same leaf by five females. Scale is in cm. B. Eggs are laid in layers. C. The egg cluster on the right is 9 or more days old and has some parasitized (black) eggs. The egg cluster on the left is 4 days old.

and, thus, benefit by spending less time searching and exposing themselves to mortality factors.

Whether the hosts or parasitoids benefit more from clustered eggs may be examined in differing but naturally-occurring group sizes of eggs. The Baltimore checkerspot (*Euphydryas phaeton* Drury; Nymphalidae) is suitable for this study because it deposits large egg clusters ($274 \text{ eggs} \pm 23 \text{ SD}$

per cluster, Stamp 1980b). Frequently females lay eggs with those of other females (Fig. 1A). Of 483 leaves with egg clusters, 18% had multiple (two or more) egg clusters (Stamp 1980b). The eggs are parasitized by an undescribed trichogrammatid wasp (David Vincent and Carll Goodpasture, unpublished). Thus, the advantages of clustering eggs can be evaluated by examining parasitism of single and multiple egg clusters on leaves. For comparison, numbers of missing eggs as an indicator of egg predation were determined also.

Materials and Methods

A population of *E. phaeton* was observed at the Conservation and Research Center of the National Zoological Park at Front Royal, Virginia in 1978 and 1979. Turtlehead (*Chelone glabra* L.: Scrophulariaceae) the larval host plant grew in wet meadows along one drainage. In each year about 500 egg clusters were deposited in this study area. Egg clusters consisted of eggs deposited usually in two layers, with a typical nymphalid egg shell and moderate adhesion to the leaf (Fig. 1B).

New egg clusters on tagged plants were photographed with Kodachrome film. The bright yellow coloration of new clusters differentiated them from older (5 to 24 days), tan to red egg clusters. Females sometimes deposited eggs adjacent to those of another female. The newer egg clusters were easily distinguished from the older clusters by coloration. The egg clusters were rephotographed 15 to 20 days later. At that time the black, parasitized eggs were readily distinguishable from the red, unparasitized eggs (Fig. 1C). From the photographs I counted the eggs to determine the original numbers deposited. Due to layering of eggs in the clusters, the margin of error for egg counts was 5.5% of the mean eggs per cluster. This was determined by photographing 32 clusters, estimating the number of eggs per cluster from the photograph, and then counting the number of eggs per cluster using a dissecting microscope.

The number of missing eggs was calculated by counting eggs in the rephotographed clusters and comparing that to the original numbers deposited. Empty egg shells and partial egg shells were classified as missing eggs. Although some of the missing eggs may have been lost due to abiotic factors (e.g. Dempster 1971, Root and Chaplin 1976), most were probably lost to predators (e.g. indirect evidence from Ives 1967; Owen 1971; Ehrlich and Gilbert 1973; Gilbert 1975; Rausher 1979a, 1979b; Stamp, pers. observ.). Thus, I considered missing eggs as representative of those eaten by predators.

To determine egg parasitism, the black eggs in the rephotographed clusters were counted. These numbers were not affected by layering of eggs because the parasitized eggs were only found in the exposed layers of the

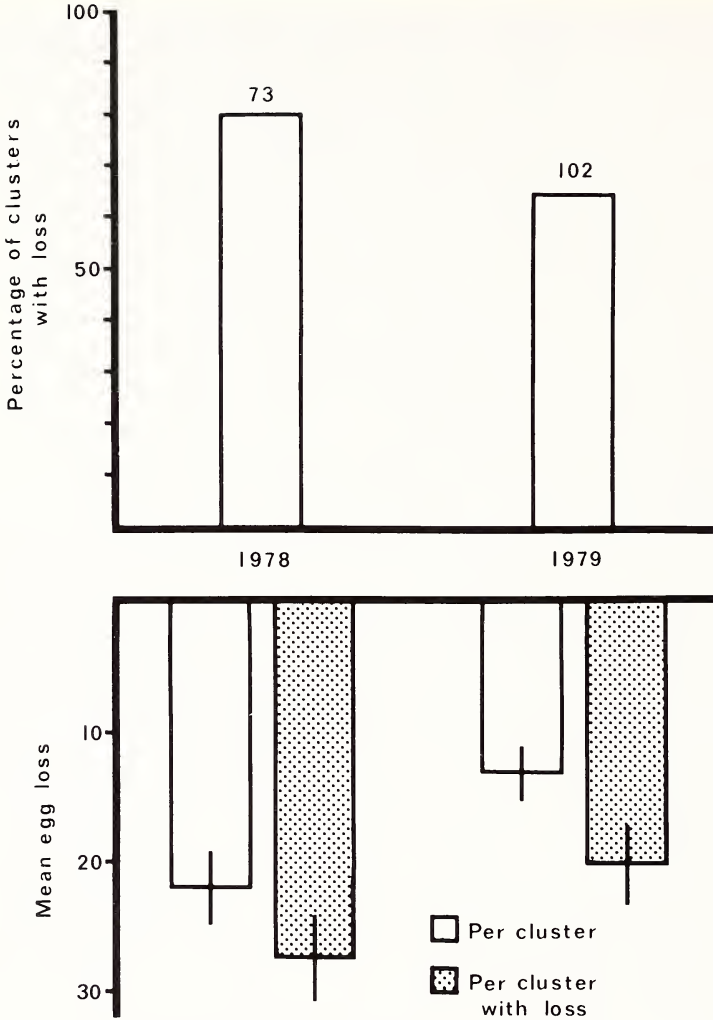


Fig. 2. Total egg loss between years. Numbers above bars are total egg clusters, and \pm one standard error is indicated for mean egg loss. The proportion of clusters with egg losses (missing and parasitized) differed significantly (χ^2 -test, $P < .05$). Mean egg loss for all clusters and mean egg loss for only those clusters with losses were both significantly different between years (all clusters, two-sample t test, $P < .001$; clusters with loss, two-sample t test, $P < .05$).

clusters. In addition, egg clusters rephotographed in late June 1979 ($n = 102$) and clusters collected two weeks later in July ($n = 120$) were examined for parasitism. For 29 leaves the sequence of clusters deposited was determined based on egg coloration. Fifteen of these leaves had one or more parasitized cluster, for a total of 19 parasitized clusters. Parasitism rates for the first cluster and clusters deposited later were compared.

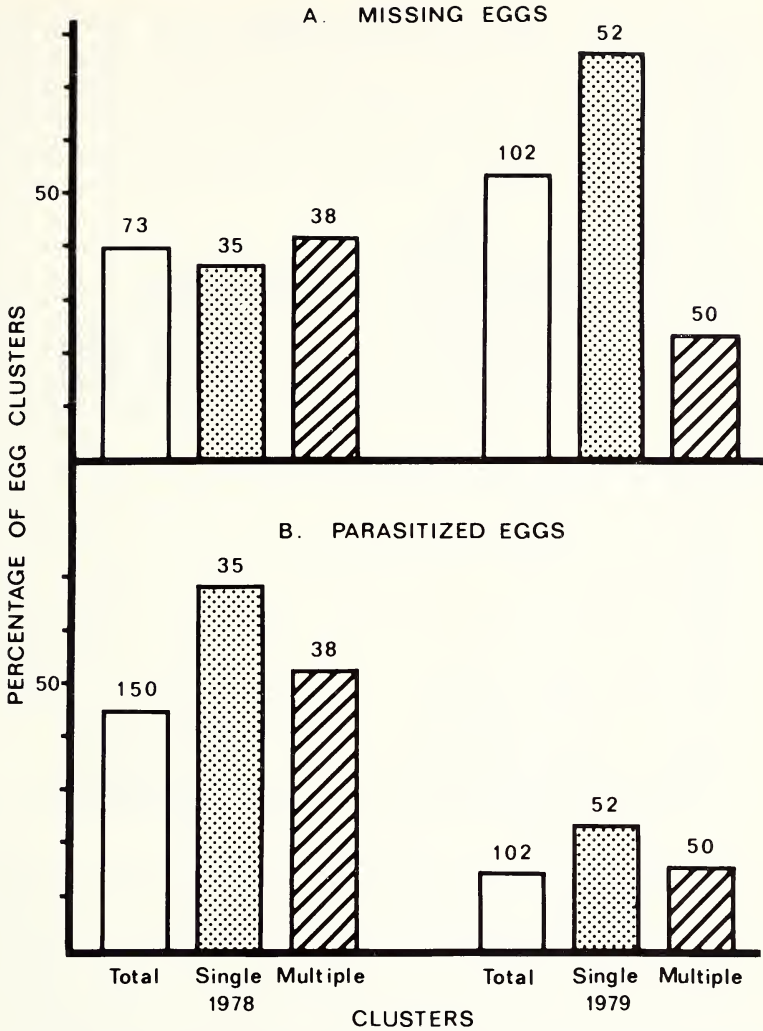


Fig. 3. Percentages of egg clusters with missing eggs and parasitized eggs. Percentages are given for total clusters, single clusters, and multiple clusters. Numbers of clusters are indicated above bars. Of the 150 clusters in 1978, 73 were classified as single or multiple clusters. A. Missing eggs: for single clusters between years, χ^2 -test, $P < .025$; for single and multiple clusters in 1979, χ^2 -test, $P < .001$. B. Parasitized eggs: for single clusters between years and for multiple clusters between years, χ^2 -tests, $P < .001$ and $P < .005$, respectively. No significant differences occurred between single and multiple clusters within years (χ^2 -tests, $P > .25$).

Results

Total clusters.—Some 65 to 80% of the clusters lost eggs (parasitism and predation), and from 5 to 9% of the eggs per cluster were lost ($n = 73$ and 102 clusters for 1978 and 1979, respectively; Fig. 2). Most clusters with egg

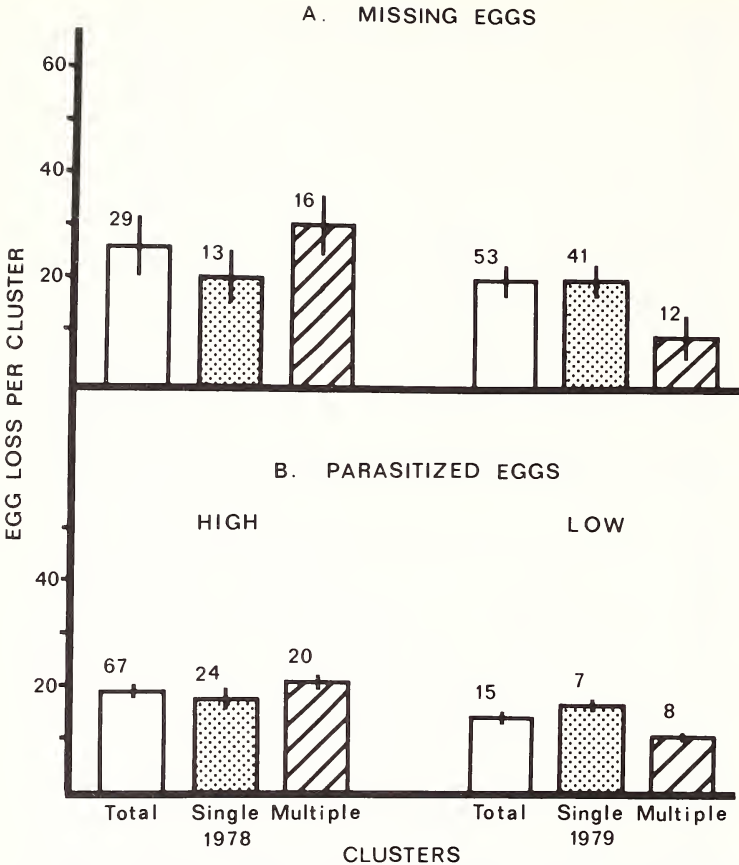


Fig. 4. Mean numbers of missing and parasitized eggs per cluster with egg loss. Means are given for total clusters, single clusters, and multiple clusters, with \pm one standard error. Numbers of clusters with egg loss are indicated above bars. Of 67 parasitized clusters in 1978, 54 were classified as single or multiple clusters. High and low refer to a relatively high or low overall rate of parasitism between years as indicated in Fig. 2B. A. Missing eggs: for single and multiple clusters in 1979, and for multiple clusters between years, Mann-Whitney U test, $P < .05$. B. Parasitized eggs: for single and multiple clusters in 1978, Mann-Whitney U test, $P < .001$; but for single and multiple clusters in 1979, Mann-Whitney U test was not significant ($P > .05$).

loss lost a few eggs (less than 20), but a few lost as many as 40 or more. The proportion of total clusters with missing eggs were similar between years, as were the mean losses per cluster (Figs. 3A and 4A). Some 4% of the eggs per cluster were missing. Chrysopid larvae, coccinellid larvae and pentatomid nymphs were observed at egg clusters. In contrast to missing eggs, the numbers of total clusters with parasitized eggs and the mean losses per cluster were significantly different between years (Figs. 3B and 4B). Generally, less than 5% of the total eggs were parasitized. During the egg

deposition period (June), clusters laid later in the month had a level of parasitism similar to those laid earlier in June (χ^2 -test, $P > .10$), but mean loss per cluster was higher in July than in June (normal approximation to Mann-Whitney U test, $n_1 = 28$ and $n_2 = 102$, $P < .001$). Thus, egg clusters attacked by predators and parasitoids and which were composed of several hundred eggs lost only about a tenth of the eggs (e.g. 27 eggs lost ± 26 SD in 1978).

Single and multiple clusters.—The proportion of egg clusters attacked by predators varied considerably between years for single clusters and between single and multiple clusters in 1979 (Fig. 3A). Egg losses due to predation also varied from year to year, with less on multiple clusters than on single clusters in 1979 (Fig. 4A).

The numbers of parasitized clusters were significantly different between years for single clusters and for multiple clusters (Fig. 3B). However, the number of egg clusters per leaf (that is, single compared to multiple clusters) had no disproportionate effect on the number of parasitized eggs per cluster (Mann-Whitney U test for 1978 and 1979 combined; $n_1 = 20$ and $n_2 = 22$ for single and multiple clusters, respectively; $P > .05$). The sequence of egg clusters deposited did not affect the level of parasitism and number of eggs parasitized (for clusters attacked, χ^2 -test, $P > .10$; for parasitized eggs, Mann-Whitney U test, $P > .10$).

Discussion

The number of parasitized eggs among *E. phaeton* clusters was probably a function mainly of three factors. 1) The distribution of *E. phaeton* clusters in these wet meadows was clumped (Stamp 1980b) and most likely was clumped relative to the parasitoids' habitat (e.g. Flanders 1937). Consequently, some egg clusters escaped parasitism and predation. More parasitized eggs in multiple clusters than in single clusters when overall egg parasitism was high suggests that these egg parasitoids may cue on the large, clumped resources of clusters. Cheke (1974) found that the area of discovery was higher for randomly dispersed egg clusters when parasitoid (*Alaptus fuscus* Haliday: Mymaridae) densities were low whereas when parasitoid densities were high, multiple clusters were attacked more efficiently. 2) The variation in numbers of eggs attacked (range 1 to 93 parasitized eggs per cluster) indicates that some clusters were used by two or more parasitoid females. 3) The age of the eggs when located by parasitoids may determine host acceptance (Lewis and Redlinger 1969, Vinson 1976). Furthermore, the change in egg coloration (yellow to red) followed by the pale green coloration of the newly-hatched larvae suggests that these eggs may contain toxins (e.g. Stamp 1980a) and, thus, such toxins may restrict the period when eggs are acceptable to parasitoids and predators.

The variation in clusters attacked by predators and loss of eggs was prob-

ably a result of the clumped distribution of egg clusters in the habitat, mobility of the egg predators (mainly nymphs and larvae rather than winged insects), and wide variety of generalist predators using these eggs. For example, the greater loss of eggs from single clusters compared to multiple clusters in 1979 but similar losses between single and multiple clusters in 1978 appeared to be a consequence of the random distribution of the set of egg predators in this habitat. Ives (1967) suggested that overall egg mortality of the larch sawfly *Pristiphora erichsonii* (Hartig) was unrelated to predator density due to the random distribution of the predators in contrast to the clumped distribution of eggs, but that once egg predators located clusters they remained near the eggs and fed periodically. The clumped distribution of missing eggs within clusters of *E. phaeton* supports this.

Finally, for *E. phaeton* females, depositing eggs with those of other females appeared to have no effect on levels of egg parasitism and predation. Perhaps later-deposited clusters benefited from nearby predators satiating themselves on the first cluster, but in one case the second cluster deposited of three on a leaf was almost completely destroyed by a predator whereas the other two clusters lost only a few eggs each. Similarly, later-deposited clusters had the same level of parasitism as the first clusters deposited per leaf. Consequently, the advantage of depositing clusters with those of other females was unrelated to the sequence of cluster deposition on a leaf. Thus, in this host-parasitoid system, egg clusters composed of several hundred eggs lost a small fraction of eggs to parasitoids and did not benefit from aggregation of egg clusters.

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